## THE ORIGIN OF CORN
### II. TEOSINTE, A HYBRID OF CORN AND TRIPSACUM
BY
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THE tripartite theory of the origin of corn (26) holds, among other things, that teosinte (*Zea mexicana*) originated as a hybrid between corn and Tripsacum, which backcrossed to corn one or more times. In 1939, the hybridization was postulated as having occurred well after corn had been domesticated, perhaps as late as 900 A.D. Reeves, however, later (35) favored the suggestion of Stebbins (47) that it might have occurred much earlier, possibly at a time when corn and Tripsacum possessed somewhat the same plant characters as now but when they were more interfertile. Mangelsdorf and Smith (28) reported archaeological evidence that teosinte came into existence not later than 500 B.C. and perhaps earlier.

Both Weatherwax (51, 52, 53) and Randolph (31, 32) raised objections to this part of the theory, objections which fall into the following categories: (A) A cross as difficult to make as that of corn and Tripsacum could not have occurred in nature. (B) Tripsacum chromosomes and genes have a negligible effect when in combination with corn germplasm. (C) The frequency of interchange or crossing over between corn and Tripsacum is not sufficient to give rise to a new intermediate species by intro-

gression. (D) The apparent relationship of chromosome-knob numbers with geographical distribution is a fallacy or is not pertinent to the problem. (E) The chromosomal characters of corn, teosinte, and Tripsacum are not consistent with the theory that teosinte originated as a hybrid between corn and Tripsacum. (F) There is no cytological mechanism by which the terminal knobs of Tripsacum could have assumed the internal positions now found in some varieties of teosinte. (G) The fact that teosinte is intermediate between corn and Tripsacum in plant characters is of minor importance.

These objections will be considered in the order named, with emphasis on recent results obtained by various investigators; for completeness two additional topics will be discussed.

### POSSIBILITY OF NATURAL HYBRIDIZATION OF CORN AND TRIPSACUM

The first crosses of corn by Tripsacum, on which our earlier studies were based, were made only after removing the shucks of corn and pruning the silks. But we have found since 1939, as Randolph also has, that the pruning of the silks, although probably helpful, is not essential to hybridization.

Since they appear to have been overlooked, we shall repeat two possibilities previously mentioned (26) by which corn might become hybridized naturally with Tripsacum: (a) the occurrence of ears which protrude beyond the shucks, a common character in certain varieties; (b) silks exposed to the base through mutilation of the shucks by insects or by holes bored by larvae.

Weatherwax's own publications (51, 52, 53) mention or describe at least four additional conditions in corn—depauperate plants with terminal pistillate inflorescences, homozygous pod corn, flowering tillers and his hypo-

thetical ancestor of modern corn—in which the silks are exposed to pollen for their entire length. Also from Weatherwax's laboratory has come what is perhaps the most significant evidence on this point. Farquharson (14) demonstrated that certain varieties of Tripsacum, when used as female parents, crossed readily with corn without the use of special techniques. She states: "In fact, it seems highly probable that this cross has occurred occasionally in nature."

Randolph's objection to this part of our theory is based on his own experiments in crossing Mexican and Guatemalan varieties of corn with Mexican and Guatemalan Tripsacum. Although these experiments may seem to have the virtue of directness, they are far from critical in several respects. The number of ears pollinated, 612, seems impressive at first glance, but a critical analysis suggests that successful crossing on a scale proportional to the numbers involved could hardly have been expected, especially because of the high frequency in these areas of the $Ga$ gene which produces cross sterility. These experiments likewise fail to take into account two important facts: (a) that the corn and Tripsacum of today is not the same as was that of ancient times; (b) that even the modern types of corn and Tripsacum of the region have not been completely sampled.

Cutler and Anderson (11), in a survey of the genus Tripsacum, did not find *T. dactyloides* south of the United States–Mexican border. Fourteen years later, Randolph (32) stated twice that *T. dactyloides* has still not been reported south of the Mexican border and that this species therefore could not have been involved in the assumed recent hybridization with corn in Guatemala or neighboring areas. Apparently, he was not aware that Melhus (29) two years earlier had reported the occurrence of this species in Guatemala. Mangelsdorf (unpub-

[ 359 ]

lished) has identified prehistoric Tripsacum, apparently *T. dactyloides*, from El Diablo Cave, Tamaulipas, Mexico and has found the same form growing in the vicinity. A general appraisal of the evidence published to date suggests that, of all forms tested, a 2n=36 type of *T. dactyloides* is the one most likely to produce a fertile, intermediate, backcross hybrid; this has virtually all the plant characters that would be required. The main objection is that, in combination with corn varieties with which it has been tested, this type falls a little short of being sufficiently interfertile. In 1939, we (26) pointed out several additional characters which, at that time, seemed to make it unsuitable as a putative parent. Although most such characters now have been explained in accordance with the theory of hybrid origin (34), a form of Tripsacum which meets the requirements better than those now known may yet be found in the future.

It seems desirable to consider here the implications of the suggestion made by Anderson (1), and now supported by Farquharson's experimental results (13), that the form of *T. dactyloides* currently regarded as diploid might be in reality an allotetraploid. If the center of origin of Tripsacum is in Mexico or Guatemala, as both Weatherwax and Randolph conclude, it would be natural to suppose that either *T. dactyloides* (2n=36) or its parents once occurred there. In this event, one of the parents (2n=18) of *T. dactyloides* and a primitive corn might be the parents of teosinte (47). However, we do not wish to base the case for the hybrid origin of teosinte on ancestors still unknown or now extinct. Rather we would emphasize that teosinte could be derived through the hybridization of existing forms.

THE EFFECTS OF TRIPSACUM CHROMOSOMES AND GENES

In our first hybrids between corn and Tripsacum (26),

the only functional gametes of $F_1$ plants were unreduced, and repeated backcrossing to corn produced progenies which segregated for 2n and 2n+1 classes. The extra chromosome of the 2n+1 plants no doubt was derived originally from Tripsacum, and the two genoms of both classes of plants were originally corn chromosomes. In pachytene and diakinesis of the 2n+1 plants, the extra chromosome synapsed in low frequency with one of the pairs of corn chromosomes, forming a trisome. In other plants where several Tripsacum chromosomes were present, weak synapsis occurred between additional corn and Tripsacum chromosomes. Genetical results showed that an allele of $su_1$, not completely dominant to $su_1$ of corn, was transferred from Tripsacum to corn chromosome 4. In vegetative characters, the 2n+1 plants were so different from their 2n sibs that the two classes could usually be distinguished at a glance. The presence of a single Tripsacum chromosome resulted in partial sterility, both male and female.[1]

The work of Maguire (21, 22) confirmed the salient cytogenetical features reviewed above, except that in her stocks one extra Tripsacum chromosome produced only a negligible effect on the corn phenotype and no reduction in ear fertility. In light of the possibility that the forms of Tripsacum with 36 somatic chromosomes might actually be tetraploids, as Farquharson's (13) work strongly indicates, the results obtained by Maguire, and especially an interpretation placed on them by Randolph, are in need of review.

Maguire's cytological material consisted of seven stocks, which she stated were possibly distinct in the

[1] In an earlier publication (26), we attempted to estimate the number of Tripsacum chromosomes present from the degree of pollen sterility. We have since become convinced from Maguire's studies, as well as our own, that this method has little, if any, value.

sense that each stock may have had a different Tripsa-
cum chromosome. She (21) explained that it was impos-
sible to determine how many of the seven were really
different. Randolph (32) stated positively that the stocks
were trisomic for seven different Tripsacum chromo-
somes. Maguire's results justify her cautious statement
that the seven stocks were "possibly" distinct. She stated
repeatedly that her Tripsacum chromosomes number 4
and 5 were very similar to one another and that they re-
sembled B-chromosomes, although the Tripsacum parent
had only 36 chromosomes and the corn parent had no
B-chromosomes. In addition, her numbers 2, 6 and 9
were similar to each other in size, morphology, behavior
and effect on pollen sterility. We venture the opinion
that her seven stocks contained no more than four differ-
ent Tripsacum chromosomes, possibly even fewer. A final
conclusion on this question must await better evidence;
in the meantime, there is serious doubt that Tripsacum
contains seven different chromosomes, all without pheno-
typic expression in the presence of two corn genoms.

In this connection, a brief review of unpublished ex-
perimental results obtained by Reeves on a population
of corn-Tripsacum hybrids may be useful. During the
season of 1955, 45 hybrid plants of Texas Inbred 203 ×
diploid *Tripsacum dactyloides*, backcrossed three times
to Inbred 203, were grown. Cytological examination
was made on 17 of them taken at random, and each plant
examined contained one extra chromosome, sometimes
with additional irregularities. None of the 45 plants de-
hisced any pollen. When anthers of each plant were dis-
sected for pollen examination, no more than a dubious
trace of starch was found in any of the many thousands
of grains examined, and about 99 per cent of them were
completely empty. The greatest number of seeds pro-
duced by any of the 45 plants was 98, and the average

was 28.6, although each plant was pollinated several times with corn pollen.

Data taken on phenotypic characters of these BC3 plants revealed several significant differences between this population and Inbred 203, the only corn line which had entered the ancestry of the hybrids, but we shall discuss only one of these—number of rows of alicoles. This character is not only one by which the parents of this cross differ, but it is also one of the generic characters distinguishing corn and Tripsacum. With all the plants growing in the same relatively uniform nursery, planted the same day and given the same treatment, Inbred 203 had a mean of 6.48 rows of alicoles and the BC3 hybrids a mean of 4.38. This difference was highly significant statistically, and the deviation of the hybrids from their corn parent was in the direction of Tripsacum.

During the 1956 season, 290 offspring resulting from the fourth backcross to Inbred 203 were grown, and, except for a few differences which will be pointed out, the results were essentially a repetiton of those obtained in 1955. The mean number of alicole rows for Inbred 203 in 1956 was 6.36 and that for the hybrids 4.15, and again the difference between the means was highly significant. Although 288 plants of this population of 290 were completely pollen sterile and showed no greater ovule fertility than did the third backcross generation, two plants dehisced an abundance of pollen and produced approximately full ears of grains when selfed. The ear of one of these fertile plants had six rows of alicoles and that of the other seven rows, both numbers near the average of Inbred 203. It might be of incidental interest, however, to note that in certain other characters, such as number of tassel branches and height of upper ear node, one plant or the other was not within the observed range of variation of Inbred 203; and the deviation here again

was in the direction of Tripsacum. Work on these hybrids is still in progress, and more data will be needed to explain what is occurring in them. But a tentative conclusion is justified: that all of them up to and including the sixth backcross generation, with rare exceptions, had one extra Tripsacum chromosome and showed phenotypic effects of it.

## INTERCHANGE BETWEEN CORN AND TRIPSACUM CHROMOSOMES

With respect to crossing over between corn and Tripsacum chromosomes, Maguire's (21, 22) observations, confirming our own of 1939, showed clearly that some form of exchange had occurred. Maguire (22) concluded that the end of the long arm of a Tripsacum chromosome and the end of the short arm of corn chromosome 2 are sufficiently homologous to allow apparently normal pairing, and that the terminal knob of the Tripsacum chromosome was occasionally transferred to corn chromosome 2 by some mechanism other than normal crossing over. Our earlier publication (26), which reported a gene exchange in a similar hybrid at the $su_1$ locus of corn accompanied by cytological evidence of crossing over, made no claim as to the frequency or the exact nature of such exchanges, and our hypothesis of the hybrid origin of teosinte did not, and still does not, require a decision on these questions. According to this hypothesis, a single successful hybrid between corn and Tripsacum, followed by a few exchanges at such positions in the chromosomes as to replace certain blocks of corn genes with blocks of Tripsacum genes, is all that is required. Yet Randolph (32) continues to be perturbed by the apparent fact that the association between corn and Tripsacum chromosomes is not followed by the "expected frequency" of crossing over.

[ 364 ]

Babcock (2) found a relationship closely parallel to that between teosinte and its putative parents, corn and Tripsacum, in section *Ixeridopsis* of the genus *Crepis* and drew a similar conclusion. The morphological and cytological evidence indicates that this section is transitional from genus *Crepis* to genus *Ixeris*, but its phylogenetic position hardly permitted its being considered an ancestral group from which *Crepis* and *Ixeris* were derived. The somatic chromosome number of *Ixeris alpicola* and of section *Ixeridopsis* is 14, but no other group within the genus *Crepis* has this number. Babcock considered it plausible that this section resulted from hybridization between *Ixeris* and *Crepis* at a time when the present generic divergencies were not so strongly developed as now. In another section, *Pyrimachos*, the parallel is again similar to teosinte, although chromosome studies of this section had not been made at the time of Babcock's publication.

### RELATION OF CHROMOSOME KNOBS TO GEOGRAPHIC DISTRIBUTION

Reeves (33) reported a relationship between knob number and proximity to Guatemala which was statistically significant at the .05 level, when all of the 163 varieties studied were included in the analysis, and at the .01 level, when all were included except those from the Andean region. This difference in levels of significance indicated that the Andean region occupied some kind of special position in the pattern; that, were it not for samples from this region, the entire relationship would have been significant at the .01 level. Randolph agreed that a correlation was established, but he then questioned the value of the results. Although his objections are ambiguous, the inference is that the correlation observed might be merely one of knob number with low altitude, rather

[ 365 ]

than with proximity to Guatemala. In rebuttal, it may be stated with certainty that none of the samples were selected because of the altitude of their origin. That the high average knob number for Guatemala is not seriously in error is shown by Reeves' comparison of his samples with those of Mangelsdorf and Cameron (23), for which data on altitude were given. Facts presented in the following paragraph indicate that the relationship observed between knob number and proximity to Guatemala in samples originating in the United States is causal. It is possible that some selectivity for low knob number did occur in the Andean region because of the prevailingly high altitude there, but it is especially noteworthy that the inclusion of the data for this region did not strengthen the observed relationship but rather weakened it. It is, therefore, reasonably clear that the samples were taken from altitudes at random and that altitude was not *per se* responsible for the relationship observed. This conclusion is, of course, based in part on the assumption that there is no positive relationship between low altitude and proximity to Guatemala. If such a relationship does exist, it is not detectable in relief maps, and, in fact, it almost certainly is non-existent. All of these facts are given, and some of them are strongly emphasized, in the literature cited on this topic by Randolph. It is unfortunate that Randolph overlooked these additional facts when he raised his objections.

Longley (18), working with corn of the United States, showed that there exists a pronounced relationship between knob number and proximity to the Mexican border, even when only the high altitude states of Montana, Idaho, Utah, Colorado, Arizona and New Mexico are taken into consideration. Or, if all of the states from which he took samples, regardless of altitude, are considered, there is even then a relationship. Longley rec-

ognized the relationship and mentioned it several times. Weatherwax (51) stated without reservation: "The average number of knobs in maize varieties decreases with the distance north or south from Central America —that is, with distance from the area where contamination with teosinte is most likely to occur." So far as we are aware, Randolph is the only student of this problem who denies the existence of a real correlation between the number of knobs and proximity to the general region of Guatemala.

High knob number has been studied in relation to yield (50, 54) and other plant characters, but this topic will be reviewed in a separate publication (27).

We have never interpreted these correlations as "proof" (32) of recent admixtures of corn and Tripsacum. They are best explained, however, on the assumption that corn not only is older than teosinte but that it was widespread over the hemisphere before teosinte originated in Guatemala. According to this assumption, the knob-bearing chromatin of teosinte diffused through corn in all directions, by hybridization, but the greatest concentration continues to be in the vicinity where teosinte originated and still occurs.

## CHROMOSOME CHARACTERS OF CORN AND ITS RELATIVES

A great body of literature pertaining to the chromosomes of corn, teosinte and Tripsacum is in existence. Except for the significance of the number and position of knobs, this topic is relatively free from controversy, and the pertinent facts may be stated briefly.

The normal diploid chromosome number of corn is 20, and no stable aberrant numbers are known, although some varieties have supernumerary chromosomes (B-chromosomes) which behave irregularly during meiosis

[ 367 ]

and are not known to be the bearers of any specific genes. Annual teosinte has 20 chromosomes, the same as corn, and perennial teosinte 40; some varieties of teosinte also have B-chromosomes. The lowest somatic number yet reported for Tripsacum is 36, but forms with 72 have long been known, and others with 45, 54, 90 and 108 have been reported by Farquharson (13). All writers on the subject have thus far continued to designate the 36-chromosome form of Tripsacum as diploid, but most of them, in doing so, probably recognize the possibility that it may be tetraploid.

As to chromosome length and arm ratio, a majority of the corn varieties are essentially similar to one another and may be designated for convenience as "normal." The normal type is described and diagramed by Rhoades (39). Numerous aberrants are also known, some of them resulting from recent structural changes and others being of unknown origin. In these characteristics, the chromosomes of teosinte are usually similar to those of corn, but there are conflicting reports on this question (32). Longley (20) found that the synapsed pachytene homologues of an $F_1$ corn-teosinte hybrid were not significantly different from each other, and Randolph (32) accepts Longley's results as justification for a final conclusion. However, Brown (6), working with hybrids of an entirely different plant, *Gossypium*, showed that paired pachytene chromosomes of different genom groups are equal in length, despite differential size at metaphase, thus casting some doubt on the decisiveness of Longley's results even before Randolph's paper was published. The chromosomes of Tripsacum are so different from those of corn or teosinte in size and arm ratio as to defy a brief comparison. In general, they are much shorter and show many differences in arm ratio.

The number of chromosome knobs varies in corn, teo-

sinte and Tripsacum according to species and strains, but neither average numbers nor exact ranges in numbers for the various groups have yet been adequately determined. The most recent chromosome-knob count which has come to our attention for *T. dactyloides* (n= 18) is 22 to 26 (32). This is greater than any number yet reported for corn or teosinte, and even if this form of Tripsacum be regarded as tetraploid, its number of knobs per genom of nine chromosomes is greater than the average of either corn or teosinte. As to corn and teosinte, perhaps the statement will stand without contradiction that, broadly speaking, corn has the lowest number and annual teosinte an intermediate number.

As to position of knobs, those of *T. dactyloides* have a strong tendency to be terminal, but Ting (49) has shown that in another form of Tripsacum some of them are obviously intercalary. Most of the knobs of corn are intercalary, but a few are terminal; the most common position is sub-terminal, or at least closer to the end than to the centromere. Annual teosinte is again intermediate; more of its knobs are terminal than in corn, but more are intercalary than in *Tripsacum dactyloides*. Many varieties show pronounced differences in this character; according to Longley (17), the knobs of the Guatemalan varieties from Progresso, Moyuta, Nojoyo and San Antonio Huixta are mostly terminal, but those of the Mexican varieties from Durango and Chapingo are more often intercalary, like those of corn. The intermediate position occupied by teosinte, in both number and position of chromosome knobs, is one of the several characters which may be explained by the view that teosinte is a hybrid combination of knobless, pure corn and a form of Tripsacum similar to *T. dactyloides* with many knobs.

No objection to the view that teosinte occupies an intermediate position in these respects has come to our

attention, and Weatherwax (51) accepts it as a fact. Randolph (31, 32) does point out that *T. maizar* and *T. australe* are knobless or nearly so, and since he assumes that these are the only diploid Tripsacums native to Mexico and Guatemala, he concludes that any species of Tripsacum which might have hybridized with corn to produce teosinte must have been a knobless form. But it has already been explained that there are reasons for the opinion that *T. dactyloides*, or possibly one of its parents, was present in or near Guatemala in prehistoric times.

An objection has been raised (31) that the hybrid origin of teosinte requires its chromosomes to be intermediate between those of its putative parents in length and number. This objection is not valid. What should be expected does occur: the chromosomes of teosinte are similar in length and number to those of its hypothetical recurrent parent, corn. It is also important to note that Maguire's (21, 22) reports of exchanges between corn and Tripsacum chromosomes do not indicate that length and number of chromosomes were affected.

Objections to the hypothesis of the hybrid origin of teosinte have been made (31, 32) on the additional grounds that the chromosomes of teosinte are "so similar to those of corn and so dissimilar to those of Tripsacum that it seems highly improbable an exchange of segments could have occurred on a sufficiently extensive scale to account for the hybrid origin of teosinte . . ." The discussion immediately preceding the section which is here quoted shows that the writer was referring to similarities and dissimilarities in length and arm ratio. But there is no known reason why such differences should prevent the exchange of segments. It is well known, for example, that in heterozygous translocation stocks of corn, chromosomes differing widely in length and arm

ratio do synapse and exchange segments. The fact that corn and Tripsacum can be hybridized betokens some measure of homology between their chromosomes; and if this homology does exist, differences in length and arm ratio need not prevent the exchange of segments. Just how extensive this exchange should be to meet the requirements of the hypothesis of the hybrid origin of teosinte is impossible to estimate. But, if the rate were extensive, in the sense of being unrestricted or only slightly restricted, we should expect corn and Tripsacum to have merged into one continuous though highly variable group, with little or no barrier separating the parental species from each other or from their hybrids.

Weatherwax (53) states that polyembryony, apomixis and chromosomal variation in Tripsacum, as reported by Farquharson, serve to increase the doubt that a corn-Tripsacum cross could have given rise to the "stable and relatively uniform plant that teosinte is." Such an opinion needs some expansion in order to be convincing, for Weatherwax makes no attempt to point out whether or not it is based on any cytological or genetical principle. In its present form, this opinion is another *non sequitur* requiring no further discussion here.

### The Transfer of Chromosome Knobs from Tripsacum to Teosinte and Corn

Extensive objections (31, 32) have been raised to our view that chromosome knobs have been transferred from Tripsacum through teosinte to corn, on the grounds that the knobs are mostly terminal in Tripsacum but mostly intercalary in corn, and that such a transfer would require chromosomal rearrangements, for which there is little evidence.

We have stated at least twice (26, 36) that if it were explained how corn, monophyletic as it is sometimes

[ 371 ]

claimed to be, has come to have different numbers of knob positions without extensive chromosomal rearrangements, perhaps a fraction of the problem of the origin of corn would be solved. But there is as yet no explanation. Longley (19, 20) interpreted his data as supporting the hypothesis of a series of inherited gradients. However, this hypothesis has been discredited by Mangelsdorf and Cameron (23) and by Rhoades (41) in several ways. Rhoades points out, for example, that the interpretation is without experimental evidence and is contradictory to the often observed fact that when a knob is shifted by rearrangement from one position to another its appearance does not change. Randolph (32) contributes a single sentence which constitutes his most positive explanation:

The present status of the problem concerning differences with respect to the prevalence of terminal and intercalary chromosome knobs in corn, teosinte and Tripsacum forces one to the conclusion that gene mutation rather than hybridization accompanied by structural chromosomal alterations has produced these fundamental differences in chromosome morphology.

He then states that his conclusion is similar to that of Longley (19) but does not sufficiently expand his idea to make it clear and convincing. So far as his explanation goes, it is very well in agreement with the theory that teosinte is a hybrid; it simply means that teosinte is intermediate between corn and Tripsacum for *genes* controlling number and position of chromosome knobs. But Randolph's explanation seems to meet with the same difficulties that Rhoades pointed out with respect to Longley's.

Randolph's (32) favorable attitude towards the view that modern corn is a composite of several wild species of *Zea* might have been intended as a possible explanation of the various knob numbers and positions now known. But even so, it contributes nothing towards a

[ 372 ]

solution to the problem, for, according to the theory of common ancestry, all corn, as well as teosinte and Tripsacum, is traceable eventually to a single ancestor, even though the line of descent might pass through one or more intermediate ancestral forms. Somewhere in such a line of descent there must have arisen many changes in number and position of knobs. Yet Randolph insists that, according to the tripartite theory, structural rearrangements would be required to account for the different knob positions, without recognizing that they would be required equally by the theory of common ancestry.

A few literature reports will now be mentioned indicating that some varieties of corn contain structural chromosomal differences not usually recognized. Rhoades and Dempsey (42), working on 90 exotic races of corn, did not find indications of large structural differences among races when pollen abortion was used as the index, but they did find significant differences in the amount of crossing over in heterozygotes involving diverse races. Ono and Suzuki (30) found six different karyotypes in 11 corn accessions out of 69 from Nepal, the karyotypes differing in total length or in arm ratio, or both, in certain chromosomes. Blanco (5) reported various structural abnormalities in corn, following self fertilization and subsequent crossing. Clark (9) recognized six translocations and two inversions occurring naturally among the entries in corn-yield tests at the Connecticut Agricultural Experiment Station in a single season.

No final conclusion has been reached, except by Randolph (32), that abnormal chromosome 10 is anything other than the result of a simple attachment of a natural end of chromosome 10 to a fragment of another chromosome. Such an attachment to a terminal knob would change the position of the knob from terminal to inter-

calary and may serve to illustrate a possible mechanism by which some of the knobs which were once terminal became subterminal.

Abnormal chromosome 10 differs from normal chromosome 10 in the greater length of its long arm and in the greater proportion of heteropycnotic chromatin in its distal segment. Longley (17) reported this type of chromosome in corn and Chapingo teosinte and gave two possibilities as to its origin:

The origin of the much-knobbed, longer types of chromosome X might be the result of the addition of a fragment marked by both a terminal and an internal knob, or the picture might be reversed by considering that the normal short types have resulted from the loss of a terminal portion of the long arm of the long types.

There can be no doubt as to the meaning Longley intended to convey—that one of the two possibilities was the simple addition of a fragment. Longley (18) continued to refer to this type in corn as having "an additional piece on the end of the long arm," without revising his original explanation. It may be noted that Longley's interpretation of the origin of this chromosome was given in 1937, five years after Burnham's (7) discovery that a certain translocation previously reported as simple was in reality reciprocal, and three years after Sharp (44) had stated that Burnham's discovery "naturally raises a question regarding other supposed simple translocations." In other words, Longley's suggestion that abnormal chromosome 10 might be the result of the simple addition of a fragment naturally leads to the inference that he was aware of the widespread belief that broken ends are incapable of attaching themselves to natural ends, but that he regarded this case as an exception to the rule. Randolph himself recently (31, 32) contributed what might be regarded as two different views on the question. In the first paper cited, he states that normal ends "ordinarily" do

not fuse with broken ends; but, in the second paper, published after Reeves (36) had made use of Longley's interpretation as a possible illustration of how terminal knobs might become intercalary, he states: ". . . it is a well-known fact that chromosome fusion occurs only between recently broken ends . . ." And referring to the additional chromatin in abnormal chromosome 10, he states: "It is a segment that has replaced the terminal one-sixth of the long arm of chromosome 10, as Rhoades (40) has clearly shown."

The facts are that Rhoades (38, 40) discussed the question of the origin of abnormal chromosome 10 and later (41) referred to it again, without stating a conclusion. He did point out that a short terminal region of abnormal chromosome 10 has a chromomere pattern differing from that of the corresponding region of normal 10, and that crossing over is reduced in this region. This might indicate that abnormal 10 originated by the replacement of a short terminal segment with a much longer non-homologous segment. But he pointed out that this explanation would require plants homozygous for abnormal chromosome 10 to be homozygous deficient for certain loci found in the terminal region of normal chromosome 10. This is unlikely, because plants homozygous for abnormal chromosome 10 are not noticeably different in phenotype from their sibs carrying only the normal chromosome 10.

Recently, Ting (48) reported cytological evidence indicating that an abnormal chromosome 10 did originate by simple translocation. A fragment, containing a centromere, of a B-chromosome became attached to the natural end of the long arm of chromosome 10.

In the absence of a completely satisfactory explanation, however, it may be said that the tripartite theory accounts for the fact that the number of knobs in teosinte

is intermediate between the numbers in corn and Trip-
sacum better than does the theory of common ancestry.
It accounts much better for the apparent fact that teo-
sinte is intermediate between corn and Tripsacum, at
least in a broad sense, in position of the knobs.

## TEOSINTE INTERMEDIATE IN PLANT CHARACTERS

One important category of circumstantial evidence for
the hybrid origin of teosinte shows that teosinte has few
if any plant characters of its own; it is either intermedi-
ate between corn and Tripsacum or similar to one or the
other in essentially all of its characters. The significance
of this fact has been almost completely overlooked.
Randolph (32) makes a fleeting reference to it, but states
merely that the "very stable cytological features," which
are discussed on previous pages of the present paper, are
more important.

Thirty-two characters, in addition to those of chromo-
some morphology, which usually distinguish corn from
Tripsacum, were listed by Mangelsdorf and Reeves (26).
Reeves later (35) studied 23 characters, two of which
were repetitions of the 32 previously studied. In the 53
characters thus examined, teosinte is either intermediate
between corn and Tripsacum or very similar to one of
them, with two doubtful exceptions. Teosinte was actu-
ally intermediate in one of the characters designated as
exceptional—frequency of large leaf hairs—but the dif-
ferences between corn, teosinte and Tripsacum were not
statistically significant, and this character, therefore,
does not constitute a true exception. In the other ex-
ceptional character—depth of alveolus of the rachis—
Tripsacum appeared to be intermediate between corn and
teosinte, teosinte having the deepest alveolus of the three.
It was recognized that for eight of these characters, the
plant samples were too small for completely dependable

results, but even if these eight characters were ignored, which would not be fully justified, 43 characters are left which support the hypothesis of the hybrid origin of teosinte as against one which apparently does not. This single exception—depth of alveolus—might be accounted for in any of several ways, the most plausible being gene interaction.

Mangelsdorf and Reeves (26) stated that neither *T. dactyloides* nor Andean corn was known to have the freely-branching tassel of teosinte and that, in this character, therefore, they would fall short of being satisfactory putative parents of teosinte. Since that time, however, Reeves (34) has pointed out that the tassels of some varieties of Andean corn are very profusely branched. Hence, *T. dactyloides* is not ruled out because it lacks a freely-branching tassel. It should be emphasized that the list of characters studied (26, 35) includes those of the floral organs and inflorescences, which are conventionally recognized in this alliance as generic characters.

This intermediate position of teosinte is a peculiar condition which has not been explained, and which apparently cannot be explained, by divergent evolution of the three taxa from a common ancestor. If the relationship held true for only one or very few characters, it might be dismissed as being of no importance; since it holds for a large number of them, it strongly suggests that teosinte actually inherited its characters from corn and Tripsacum.

### Evidence from Fossil and Archaeological Maize

The evidence from both fossil and archaeological remains is best explained by the theory of a hybrid origin of teosinte, for it suggests that teosinte appeared on the scene more recently than either corn or Tripsacum and only after agriculture had become well established.

Barghoorn *et al* (4) identified fossil pollen grains of both corn and Tripsacum isolated from drill cores taken at a depth of more than 69 meters below the present site of Mexico City. Pollen grains thought to be those of teosinte were found also but only at levels above 3.6 meters[2] which were probably laid down after agriculture had become established in the Valley of Mexico. Barghoorn *et al* also point out that teosinte pollen is intermediate between corn and Tripsacum pollen, not only in its diameter but also, and perhaps more significantly, in the ratio of diameter of pore to the long axis. They conclude that this intermediate value is well in harmony with the postulated hybrid origin of teosinte.

Virtually all of the archaeological corn so far studied shows that teosinte introgression, when it can be recognized, made its appearance only after pure corn had been grown for some time. Mangelsdorf and Smith (28) found no evidence of teosinte introgression in the lower levels of Bat Cave, although such introgression was conspicuous in the upper four levels. Cutler's (10) descriptions and illustrations of prehistoric specimens from Tularosa Cave show that the typical corn from the lower pre-pottery levels is non-tripsacoid, while some of the specimens from the higher levels are strongly tripsacoid.

The prehistoric corn from the lower levels of La Perra Cave in Mexico (25) had predominantly non-tripsacoid glumes, while that from the uppermost level had a high proportion of cobs with tripsacoid glumes. The most tripsacoid cob in the entire collection occurred in the highest level.

Mangelsdorf and Lister (24) reported that tripsacoid cobs occur in the upper levels of Swallow Cave in north-

[2] Weatherwax (53) is clearly in error in stating that teosinte pollen was found at depths of more than 150 feet. Randolph, the joint author of the same chapter, correctly states that no teosinte pollen was found at levels below 3.6 meters.

western Mexico and are found in three other caves — Slab, Tau and Olla—in the State of Chihuahua. Nontripsacoid maize resembling a Mexican race, Chapalote, was found in the lower levels of Swallow Cave.

Galinat *et al* (16) found tripsacoid cobs to be quite common among the prehistoric specimens from Richards Cave and Tonto Cave in Arizona. Both sites are regarded as relatively late. Galinat (unpublished) found also that the early maize from Cebollita Cave in New Mexico is not tripsacoid, while later maize includes many specimens showing teosinte introgression.

The six studies on archaeological maize reviewed above, only one of which was known to Weatherwax and Randolph, as well as the data on fossil pollen, support the theory that teosinte, because it is a hybrid of Tripsacum and cultivated maize, came into existence only after the cultivation of maize was well established.

### TAXONOMIC STATUS OF TEOSINTE

When the transfer of the two species of *Euchlaena* to the genus *Zea* was published (37), it was made clear, we believe, that our previous conclusion as to the origin of teosinte did not influence our conviction that the groups should be made congeneric—that the transfer was justified regardless of the manner of the origin of teosinte or corn. Weatherwax (52, 53) and Randolph (31, 32) have overlooked or ignored these statements and have repeatedly confused the taxonomic change with the issue of the origin of teosinte. If we could agree with their theory that corn and teosinte originated by divergent evolution, our conviction that the two groups ought to be regarded as congeneric would not be weakened in the least.

Randolph himself (32) recognizes that hybrid intergrades between corn and teosinte do occur naturally and describes the intergradation as occurring in the very same

characters which he contends are stable and of generic value. He recognizes also that their cytogenetical relationships really approach those of a single species. He reaches the somewhat conflicting conclusions that the characters by which corn and teosinte differ are generic; but that teosinte is maintaining its identity as a "good species." His statement that corn and teosinte are more distinct entities than many other genera of the grass family is vague, and he offers no examples of such genera. Numerous examples are on record of separate genera comprising certain species which are scarcely distinct. To mention only one such case: Fisher, Bashaw and Holt (15) found *Pennisetum ciliare* (L.) Link and *Cenchrus setigerus* Vahl. to be nearly or quite inseparable by either morphological or cytological characters and suggested that the forms examined belong to a single agamic complex, but by no means did they indicate satisfaction with the present taxonomic status of this group. It may be safely stated that plant taxonomists generally are dissatisfied with the classification of such groups. The reason why solutions have not yet been offered for these confusing complexes is that they have not been worked out.

Various degrees of approval of the consolidation of *Zea* and *Euchlaena* have been brought to our attention, although we have not canvassed the literature for examples of this. Sharp (45) reviews the salient facts and states: "This indicates a degree of cytological and genetical similarity unusually high for plants assigned to different genera." Stebbins (47) refers to teosinte as *Zea* (*Euchlaena*) *mexicana*, and Celarier (8) takes a strong position that the transfer is justified. Rollins (43), after reviewing the evidence relative to this problem, states that the two groups are congeneric and that Reeves and Mangelsdorf have rightly transferred *Euchlaena* to *Zea*. Darlington (12) goes even further and insists that *Zea*

and *Euchlaena* ought to be made conspecific, an idea which we had earlier (37) considered but rejected, giving our reasons for doing so. Darlington does not seem to be aware of our publication. Sinnott, Dunn, and Dobzhansky (46) refer to annual teosinte as *Zea mexicana* without reservation. In view of the above facts, Weatherwax's (53) statement that our "proposal has met with little favor" is somewhat erroneous to say the least.

The actual issue involved is whether or not natural relationships as indicated by cytogenetical behavior and gene exchange without the use of artificial techniques are to be recognized in taxonomic treatments. If they are to be recognized, there can be no doubt that the consolidation of *Zea* and *Euchlaena* is justified.

## SUMMARY

The circumstantial evidence that teosinte originated as a hybrid between corn and Tripsacum is substantially stronger now than in 1939, when the idea was first proposed, for the following reasons: Not only has the cross between corn and Tripsacum been successfully repeated, but it has been made without special techniques. The species of Tripsacum (*T. dactyloides*) which has come nearest to showing introgression with corn under experimental control has been reported in Guatemala, where teosinte is believed to have originated and where corn is known to have been abundant since ancient times. There is increasing evidence, also, that *T. dactyloides* or forms similar to it, previously were more common in the area than they are now.

Tripsacum genes have been demonstrated to have a phenotypic effect in corn-Tripsacum hybrids, a natural supposition which was once doubted by some students of this problem. The first report of crossing over between

corn and Tripsacum chromosomes, when associated in the same nucleus, has been confirmed.

With few exceptions, annual teosinte, the species most comparable to modern corn, proves to be intermediate between corn and Tripsacum in number and position of chromosome knobs.

It has become increasingly clear that a correlation exists in corn varieties between frequency of chromosome knobs and proximity of their native locality to Guatemala and southern Mexico. As corn and teosinte hybridize naturally, this correlation constitutes further circumstantial evidence on the phylogenetic relationship between corn and teosinte. It is explicable on the assumption that pure corn without knobs was already widespread over the American continent when teosinte originated. Later corn and teosinte began hybridizing, and, in fact, are still doing so; in this way, a slow "diffusion" of corn with knob-bearing chromosomes from Guatemala and southern Mexico has been occurring for several centuries, but an equilibrium in knob frequency throughout the continent has not been reached.

The hypothesis of the hybrid origin of teosinte has been vigorously challenged on the grounds that many of the chromosome knobs of corn are intercalary, whereas those of Tripsacum are terminal, and that changes in knob positions would require structural chromosomal rearrangements which probably have not occurred. Structural rearrangements not previously recognized have been demonstrated since 1939, however, and some forms of Tripsacum actually have been shown to possess a few internal knobs. In any event, our statement of 1939 still stands: that the theory of common ancestry is confronted with this same problem as to the origin of the different knob positions.

Considerable evidence from archaeology and paleo-

botany pertinent to the relative ages of corn, teosinte and Tripsacum indicate that teosinte is of recent origin. This also can be explained by the theory that teosinte originated as a hybrid between corn and Tripsacum.

It should be emphasized that all the facts discussed above are not merely in *agreement* with the theory of the hybrid origin of teosinte, but also that they are *explained* by this theory. The odds are extremely low that a theory can explain so many facts, drawn from so many sources, without being somewhat of an approximation of the truth. Although other current theories are not completely disproved, they do not explain so many of the facts.

The question of whether or not teosinte should be regarded as generically distinct from corn is not a part of the problem of the origin of corn or teosinte. The known facts indicate, however, that the relationship conforms best to that of congeneric species.

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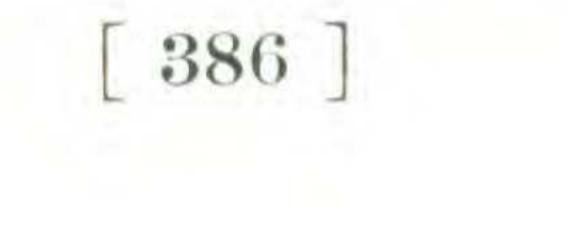11. ——— and E. Anderson, 1941. A preliminary survey of the genus Tripsacum. Ann. Missouri Bot. Gard. 28: 249–269.

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